Nontarget Effects of Transgenic Insecticidal Crops: Implications of Source-Sink Population Dynamics

MARK S. SISTERSON,[1] YVES CARRIÈRE, TIMOTHY J. DENNEHY, AND BRUCE E. TABASHNIK

Department of Entomology, University of Arizona, Tucson, AZ 85721

ABSTRACT   Widespread planting of transgenic insecticidal (TI) crops for pest control has raised concerns about potential harm to nontarget arthropods. Because the first generation of TI crops produce single *Bacillus thuringiensis* (*Bt*) toxins causing little or no harm to most nontarget arthropods, they are not likely to cause such negative effects. However, varieties of transgenic crops with multiple *Bt* toxins or novel toxins might be more harmful to nontarget arthropods. Field studies assessing nontarget effects typically compare the relative abundance of nontarget arthropods in TI crop fields to non-TI crop fields. However, for nontarget arthropods that are killed by TI crops, such analyses may miss important effects. Results from simulations of a spatially explicit population dynamics model show that large-scale planting of TI crops could cause three types of negative effects on nontarget arthropods that suffer mortality caused by TI crops: (1) lower abundance in TI fields than non-TI fields with little or no effect on abundance in non-TI fields, (2) lower abundance in TI fields than non-TI fields and decreased abundance in non-TI fields, and (3) loss of the arthropod from TI and non-TI fields. Simulation results show that factors increasing the potential for negative effects of TI crops on nontarget arthropods in non-TI fields are low reproduction, high emigration, high adoption of TI crops, high mortality in TI fields, insecticide sprays, and rotation of TI and non-TI fields. The results suggest that risk assessment should consider the regional distribution of transgenic crops and the life history traits of nontarget arthropods to identify the most vulnerable regions and nontarget species.

KEY WORDS   *Bacillus thuringiensis*, nontarget, transgenic crops, risk assessment, source-sink

Genetically engineered crops producing *Bacillus thuringiensis* (*Bt*) toxins are planted on millions of hectares worldwide (Lawrence 2005). *Bt* crops producing single toxins for insect control represent the first generation of transgenic insecticidal (TI) crops. Currently grown commercial TI crops produce one or two *Bt* toxins. TI crops of the future may produce more *Bt* toxins either alone or with other types of toxins (Ferry et al. 2006). The widespread planting of TI crops has raised concerns about potential harm to nontarget arthropods (Schuler et al. 1999, Obrycki et al. 2001, Groot and Dicke 2002, Conner et al. 2003, Carrière et al. 2004a, Sisterson and Tabashnik 2005). To address this issue, many field studies have compared the abundance of nontarget arthropods in plots or fields of TI and non-TI crops (Reed et al. 2001, Wold et al. 2001, Al-Deeb and Wilde 2003, Jasinski et al. 2003, Men et al. 2003, Sisterson et al. 2004a, Dively 2005, Naranjo 2005). Such studies define a negative effect as reduced abundance in TI fields compared with non-TI fields. Detection of negative effects is rare and inconsistent,

suggesting that currently available TI crops do not harm most nontarget arthropods (Naranjo et al. 2005). However, evaluation of TI crops will continue as new varieties are developed. Thus, consideration of methods used to assess nontarget effects may help in designing better strategies to evaluate current and future varieties of TI crops.

Current methods focus solely on detecting negative effects in TI fields, assuming implicitly that populations in non-TI fields are not affected. However, large-scale planting of TI crops can cause population declines of susceptible target pests in TI fields and non-TI fields (Riggin-Bucci and Gould 1997, Carrière et al. 2003, 2004a, Caprio et al. 2004). Although source-sink theory explains population declines of target pests in non-TI fields (Caprio 2001, Carrière et al. 2003, 2004b, Sisterson et al. 2005), this theory has not been applied previously to nontarget arthropods.

Here, we used a spatially explicit population dynamics model to assess the conditions under which TI crops could reduce nontarget arthropod populations in non-TI fields and TI fields. We also considered the consequences of such regional declines for the design and interpretation of studies evaluating the impact of TI crops on nontarget arthropods.

[1] Corresponding author: USDA–ARS, San Joaquin Valley Agricultural Sciences Center, 9611 S. Riverbend Ave., Parlier, CA 93648 (e-mail: msisterson@fresno.ars.usda.gov).

Table 1. Parameters used in simulations

Parameter	Assumptions
Varied in sensitivity analyses	
Maximum reproductive rate (r)	Low = 1.5, high = 3
Emigration (proportion leaving their natal field, e)	Low = 0.2, high = 0.8
Mortality in TI fields (m)	Low = 0.2, high = 0.6
Fields planted with TI crops (%)	0–80
Temporal distribution of TI and non-TI fields[a]	Fixed, rotated
Probability of receiving an insecticide spray[b]	0, 0.2
Fixed	
Number of fields	900
Field size	15 ha
Carrying capacity per field (K)	1,000,000
Spatial distribution of TI and non-TI fields	Random
Mortality in non-TI fields	0
Mortality per insecticide spray in treated fields	0.8

[a] With fixed fields, field types once designated did not change. With rotated fields, field types were randomly reassigned every five generations.

[b] Simulations were conducted without insecticide sprays in which case the probability a field was sprayed was zero. Simulations were also conducted with insecticide sprays in TI and non-TI fields. For these simulations, the probability of receiving an insecticide spray was 0.2 per generation for each field.

Materials and Methods

Population Dynamics, Mortality, and Movement. The model was written in C++ using Microsoft Visual C++ 2005 (Microsoft, Redmond, WA; code available from senior author on request). Table 1 summarizes the key assumptions, including those varied in sensitivity analyses. We modeled a grid of 900 fields (30 by 30). Each field was 15 ha, the average size of cotton fields in Arizona (Sisterson et al. 2004b) and planted entirely with a TI crop or a non-TI crop. Field types (i.e., TI or non-TI) were distributed randomly in the grid. Two assumptions about the temporal distribution of fields were examined. Field types were fixed for an entire simulation (fixed) or randomly reassigned every five generations (rotated).

The population dynamics in each field were independent and determined by:

$$N_{t+1} = r_r \times N_t \times (1 - m)$$

where population size in each field at generation $t + 1$ (N_{t+1}) was a function of population size at time t (N_t), realized reproductive rate (r_r), and mortality (m) in TI and non-TI fields. Mortality was 0 in non-TI fields. Two values for mortality in TI fields were used: low (m = 0.2) and high (m = 0.6). These values capture the range of effects observed in more complete sensitivity analyses where mortality in TI fields was varied from 0 to 1 (results not shown).

The realized reproductive rate (r_r) was determined by the maximum reproductive rate (r) and the carrying capacity (K):

$$r_r = r^{\left(1 - \frac{N_t}{K}\right)}.$$

When population size was zero, r_r equaled the maximum reproductive rate, r. When population size equaled the carrying capacity, r_r equaled one. Finally, when population size exceeded the carrying capacity, r_r was less than one. Density-dependent reductions in reproductive rate occurred before mortality caused by the TI crop. Source-sink theory indicates that populations in non-TI fields are more likely to decline when reproduction is low (Carrière et al. 2003). Thus, a low (r = 1.5) and high (r = 3) value was used. The carrying capacity per field (K) was 1,000,000.

Simulations were done with and without insecticide sprays in TI and non-TI fields. Sprays were applied independent of the abundance of nontarget arthropods. Each field had a 20% chance of being sprayed each generation. Sprays killed 80% of the nontarget arthropods in treated fields. In TI fields, mortality from sprays occurred after mortality from TI toxin.

After reproduction and mortality, a proportion (e) of the population emigrated to neighboring fields. Emigrants were distributed evenly in all directions from the source field. Source-sink theory indicates that populations in non-TI fields are more likely to decline with high emigration (Carrière et al. 2003). Thus, effects of low (e = 0.2) and high (e = 0.8) emigration were studied. With low emigration (e = 0.2), 80% stayed in their natal field and 20% moved a distance of one field. With high emigration (e = 0.8), 20% stayed in their natal field, 65% moved one field, 14% moved two fields, and 1% moved three fields. Emigrants that moved out of the region were lost from the system.

Equilibration Before Introduction of TI Crops. Simulations started with the population size of arthropods in each field at the carrying capacity. The model was run for 100 generations without TI fields to allow equilibration. Equilibration occurred in <10 generations, so the equilibration period of 100 generations was longer than necessary to ensure equilibration. After the equilibration period, TI fields were introduced. The model was run for up to 150 generations during which mean abundance was monitored in TI and non-TI fields.

Sensitivity Analyses. First, we studied the different types of negative effects on nontarget arthropods caused by TI crops as a function of variation in reproduction and emigration with 80% of fields occupied by TI crops, 60% mortality in TI fields, and all other factors held constant (see Table 1). Second, we systematically varied assumptions about reproduction, emigration, mortality in TI fields, the percentage of fields planted with TI crops, temporal field distribution, and insecticide use. Twenty replicates were completed for each of 192 combinations of parameters. Coefficients of variation for simulation runs with the same parameter sets were typically <5%, except in cases where abundance in non-TI fields decreased to <200,000. In most cases, abundance in TI and non-TI fields did not change between generations 50 and 150 after introduction of TI fields. Thus, we report the mean abundance of nontarget arthropods 50 generations after introduction of TI fields. We also indicate
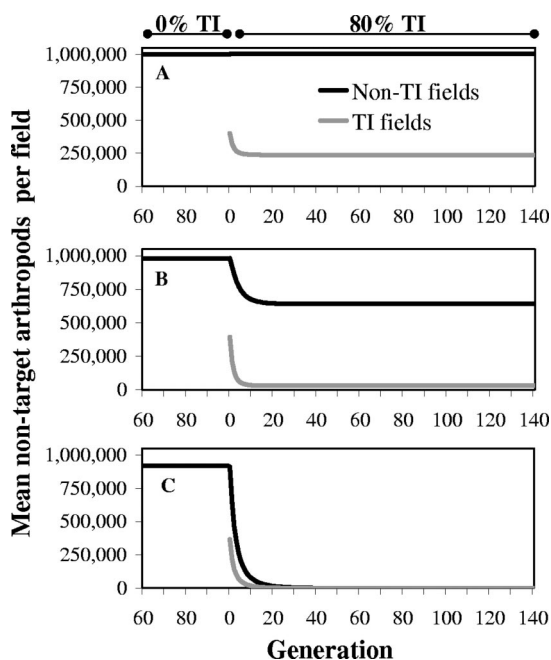
Fig. 1. Three types of negative effects on nontarget arthropod abundance caused by TI crops. Mortality in TI fields (m) was 0.6, field types were fixed, and sprays were not applied. The model was run for 100 generations for equilibration before introduction of TI crops (only the last 40 generations are shown). At generation 100, 80% of fields were randomly designated as TI fields and the generation counter was reset to zero. (A) Abundance in non-TI fields was not affected with high reproduction ($r = 3$) and low emigration ($e = 0.2$). (B) Abundance in non-TI fields decreased with low reproduction ($r = 1.5$) and low emigration ($e = 0.2$). (C) Loss from both field types occurred with low reproduction ($r = 1.5$) and high emigration ($e = 0.8$).

the exceptional cases in which means decreased by >5% between generations 50 and 150. For nontarget arthropods with five generations per year, the 50-generation period corresponds with the number of generations since the introduction of TI crops 10 yr ago.

Results

Three Types of Effects of TI Crops on Nontarget Arthropods. As expected, with a TI crop in 80% of fields and 60% nontarget arthropod mortality in TI fields, nontarget arthropod abundance was lower in TI fields than non-TI fields (Fig. 1). Under these conditions, variation in nontarget arthropod reproduction and emigration produced three general patterns of nontarget arthropod abundance: (1) lower abundance in TI fields than non-TI fields with no change in non-TI fields with high reproduction and low emigration (Fig. 1A), (2) lower abundance in TI fields than non-TI fields and decreased abundance in non-TI fields with low reproduction and low emigration (Fig. 1B), and (3) loss from TI and non-TI fields with low reproduction and high emigration (Fig. 1C). These findings

parallel previous modeling results showing decreased target pest abundance in non-TI fields with low pest reproduction and high pest emigration (Carrière et al. 2003).

Effects with Fixed, Unsprayed Fields. With 20% mortality in TI fields and high reproduction, nontarget arthropod abundance in non-TI fields was not affected by TI crops, regardless of emigration (Fig. 2A). With 20% mortality in TI fields and low reproduction, abundance in non-TI fields decreased as the percentage of fields planted with TI crops increased (Fig. 2A). This effect was stronger with high emigration (Fig. 2A). Loss from non-TI fields did not occur with 20% mortality in TI fields.

With 60% mortality in TI fields, high reproduction, and low emigration, nontarget arthropod abundance in non-TI fields was not affected by TI crops (Fig. 2B). With 60% mortality in TI fields, high reproduction, and high emigration, minor decreases in non-TI fields occurred only when the percentage of TI crops was high (Fig. 2B). Decreased, but stable, abundance in non-TI fields occurred with low reproduction and low emigration (Fig. 2B). With 60% mortality in TI fields, low reproduction, high emigration, and a high percentage of TI crops, nontarget arthropods were lost from non-TI fields (Fig. 2B).

Unsurprisingly, abundance in TI fields was higher when mortality in TI fields was 20% (Fig. 2C) than when it was 60% (Fig. 2D). For both levels of mortality, abundance in TI fields was higher when reproduction was high, whereas emigration had little effect (Fig. 2C and D).

Abundance in non-TI fields relative to TI fields was much lower with mortality in TI fields of 20 (Fig. 2E) versus 60% (Fig. 2 F). Thus, if abundance is similar in TI fields and non-TI fields, one can infer low mortality in TI fields. However, measures of relative abundance in non-TI to TI fields provided little insight into the potential effects in non-TI fields. For example, with 60% mortality in TI fields, loss from non-TI fields occurred with low reproduction, high emigration, and high adoption of TI crops (Fig. 2B), but this parameter set did not yield the highest abundance in non-TI fields relative to TI fields (Fig. 2F).

Consideration of effects in non-TI fields complicates assessment of the severity of negative effects of TI crops. For example, with 20% mortality in TI fields, low reproduction, high emigration, and 80% TI fields, abundance was 1.3 times greater in non-TI fields than in TI fields (Fig. 2E; $r = 1.5$, $e = 0.8$), and TI crops decreased abundance in non-TI fields by 32% (Fig. 2A). In contrast, with 60% mortality in TI fields, high reproduction, low emigration, and 80% TI fields, abundance in non-TI fields was 6.4 times greater than abundance in TI fields (Fig. 2F; $r = 3$, $e = 0.2$), although TI crops did not affect abundance in non-TI fields (Fig. 2B). Thus, effects of TI crops on abundance in TI fields relative to non-TI fields did not indicate effects in non-TI fields. Accordingly, current methods based on the assumption that the greater the difference in relative abundance between non-TI and TI fields the greater the negative effect of TI crops on nontarget
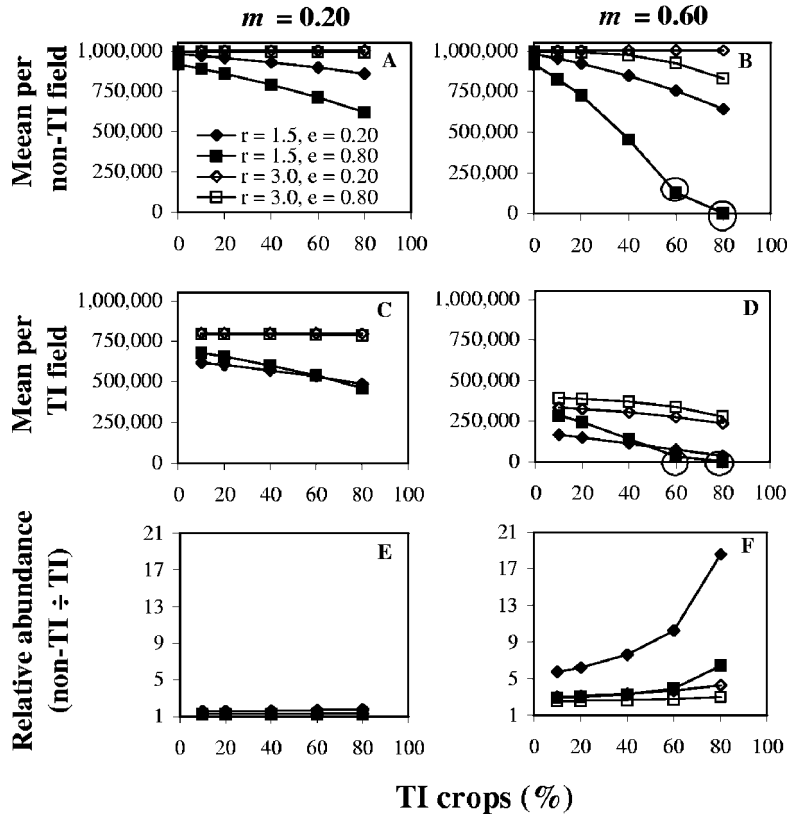
Fig. 2. Effects on the abundance of nontarget arthropods in TI and non-TI fields of percentage of fields with TI crops, reproduction (r), emigration (e), and mortality in TI fields (m). (A and B) Mean per non-TI field. (C and D) Mean per TI field. (E and F) Relative abundance in non-TI versus TI fields (mean for non-TI fields divided by mean for TI fields). Field types were fixed and sprays were not applied. Abundances shown occurred 50 generations after TI crops were introduced. Circles show conditions in which abundance decreased >5% over the next 100 generations.

arthropods could provide incomplete assessments of the impacts of TI crops under some conditions.

Effects of Sprays and Field Temporal Distribution. Simulations with insecticide sprays and fields rotated every five generations showed similar effects of mortality in TI fields, percentage of fields planted with TI crops, reproduction, and emigration on nontarget arthropod abundance compared with simulations with unsprayed, fixed fields (Figs. 2A and B and 3). For example, in all cases, abundance in non-TI fields was least affected with high reproduction and low emigration (Figs. 2A and B and 3), and abundance in non-TI fields decreased most when reproduction was low, emigration was high, and abundance of TI crops was high (Figs. 2A and B and 3). Loss from non-TI fields in 50 generations occurred only with 60% mortality in TI fields and was more likely with sprayed or rotated fields than with unsprayed or fixed fields (Figs. 2B and 3B, D, and F).

Discussion

Typical field evaluations of TI crops on nontarget arthropods compare the abundance of nontarget arthropods in TI versus non-TI fields, implicitly assuming that populations in non-TI fields are unaffected. Results of our simple, spatially explicit population dynamics model indicate that nontarget arthropods with high mortality in TI fields could experience one of three effects in non-TI fields, ranging from no effect to loss (Fig. 1). If relative abundance of a nontarget arthropod is consistently lower in TI fields relative to non-TI fields, study of effects in non-TI fields is warranted. Such tests would involve comparing the relative abundance of the nontarget arthropod in non-TI fields in areas where the use of TI crops is low to areas where it is high, similar to analyses with a target pest (Carrière et al. 2003). The results of the proposed tests would provide valuable data on whether the effect of the TI crop is localized (i.e., only observed in TI fields; Fig. 1A) or if the effect is regional (i.e., observed in TI and non-TI fields; Fig. 1B and C).

The modeling results reported here apply to herbivorous arthropods that are killed by TI plants. They also apply to natural enemies that die when eating TI-intoxicated prey or hosts, provided that prey or host abundance is similar in TI and non-TI fields and prey or host population dynamics are not tightly coupled to that of the natural enemy. The results do not apply to natural enemies that attack prey or hosts
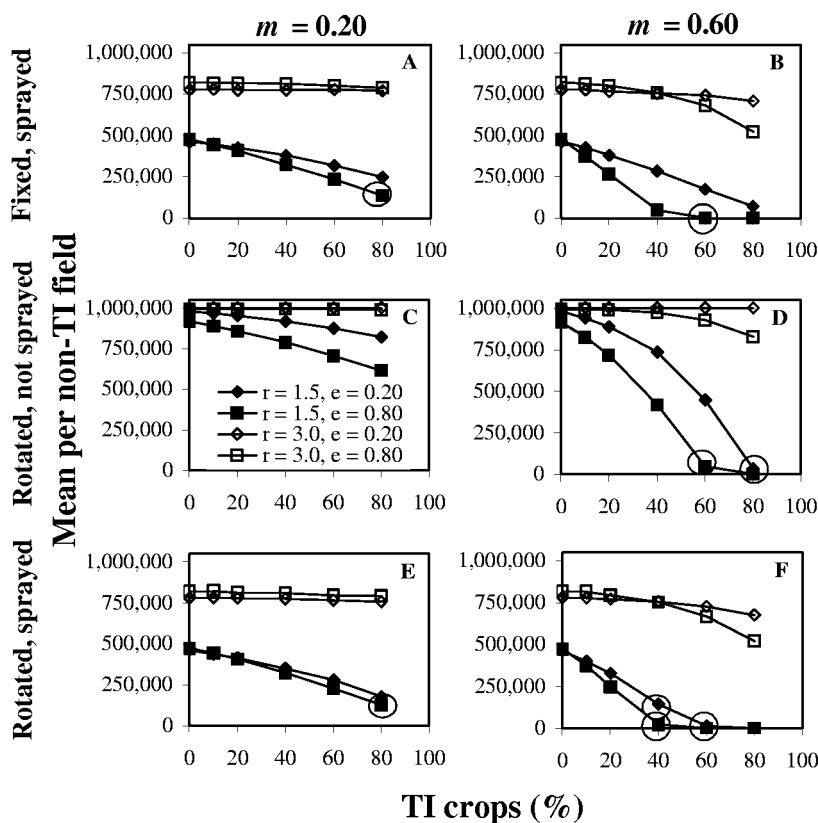
Fig. 3. Effects on the abundance of nontarget arthropods in non-TI fields of percentage of fields with TI crops, reproduction (r), emigration (e), mortality in TI fields (m), insecticide sprays, and temporal distribution of field types. (A and B) Fixed, sprayed fields. (C and D) Rotated, unsprayed fields. (E and F) Rotated, sprayed fields. Abundances shown occurred 50 generations after TI crops were introduced. Circles show conditions in which abundance decreased >5% over the next 100 generations.

whose population dynamics are strongly influenced by TI crops or the natural enemy. In such cases, interactions between prey or hosts and their natural enemies must be considered (Sisterson and Tabashnik 2005).

Effects of TI crops on abundance in non-TI fields became stronger as use of TI crops increased. For example, with 60% mortality in TI fields, only minor decreases in abundance in non-TI fields occurred with 20% TI fields, low reproduction, and high emigration (Fig. 2B). In contrast, with the same combination of mortality in TI fields, reproduction, and emigration, loss from non-TI fields occurred with 80% TI fields (Fig. 2B). The proportion of habitat composed of TI crops depends on the diet breadth of the nontarget arthropod as well as the acreage occupied by the TI crop. The proportion of habitat composed of a TI crop will be higher for specialists on that crop than for generalists that use other non-TI crops or noncultivated plants.

The simulation results reported here suggest that nontarget arthropods with high mortality in TI fields, low reproduction, and high emigration are most likely to experience declines in TI and non-TI fields (Figs. 2A and B and 3). Field studies assessing the effects of

TI crops on nontarget arthropods have examined large numbers of taxa in cropping systems. For example, Dively (2005) examined the effects of TI crops on 112 families of arthropods, Sisterson et al. (2004a) on 69 families of arthropods, and Candolfi et al. (2004) examined 76 taxa of soil dwelling arthropods, 45 taxa of plant dwelling arthropods, and 71 taxa of aerial arthropods. Such large assemblages of taxa may include species with combinations of life-history traits (i.e., low reproduction and high emigration) creating vulnerability to population declines in non-TI fields.

A prerequisite for such declines is relatively high mortality in TI fields, exhibited by lower relative abundance in TI fields compared with non-TI fields (Fig. 2E and F). Field studies have shown that some nontarget arthropods had lower abundance in TI fields compared with non-TI fields, although it is not clear if such declines were caused by toxic effects of TI crops, a shortage of prey caused by control of target pests, or a reduction of crop injury that eliminated essential resources (Dively 2005, Naranjo 2005, Whitehouse et al. 2005). Furthermore, most field studies indicate that currently used TI crops have little or no negative effect on nontarget arthropods (Reed et al. 2001, Wold et al. 2001, Al-Deeb and Wilde 2003, Jasinski et al. 2003,

Men et al. 2003, Sisterson et al. 2004a, Dively 2005, Naranjo 2005, Whitehouse et al. 2005, Cattaneo et al. 2006). Thus, regional declines in abundance of nontarget arthropods are probably rare with most currently used TI crops. However, some new types of TI crops, including those that produce more than one toxin, kill a broader range of arthropods than the first generation of TI crops. Reduced nontarget arthropod abundance in non-TI fields will be more likely if new transgenic varieties are more toxic to nontarget arthropods than current varieties.

Monitoring nontarget effects of current and future TI crops will be a complex and expensive process (Snow et al. 2005). As stated above, nontarget studies often investigate large segments of the insect community (Brooks et al. 2003, Candolfi et al. 2004, Sisterson et al. 2004a, Dively 2005, Cattaneo et al. 2006). In many cases, broad surveys are conducted to ensure that many potentially vulnerable functional groups (e.g., herbivores, natural enemies, decomposers, and seed dispersers) are represented. However, it has been proposed that systematic consideration of specific risks (e.g., importance for pest control, degree of overlap with the transgenic crop, disappearance of species of cultural value) for selecting a more restricted number of indicator species from such functional groups would represent a more cost-effective way of conducting risk assessment (Snow et al. 2005, Andow and Zwahlen 2006). Our results indicate that life history traits of nontarget organisms such as reproduction and emigration should be among the criteria used to select species most likely to be affected by transgenic crops. In addition, it was recently recommended that future risk assessment methods should take into account the regional distribution of *Bt* crops (Snow et al. 2005). Akin to such a recommendation, our results (Figs. 2 and 3) suggest that the effects of regional distribution of TI crops on nontarget arthropods should be considered.

Acknowledgments

References Cited

Al-Deeb, M. A., and G. E. Wilde. 2003. Effect of Bt corn expressing the Cry3Bb1 toxin for corn rootworm control on aboveground nontarget arthropods. Environ. Entomol. 32: 1164–1170.

Andow, D. A., and C. Zwahlen. 2006. Assessing environmental risks of transgenic plants. Ecol. Lett. 9: 196–214.

Brooks, D. R., D. A. Bohan, G. T. Champion, A. J. Haughton, C. Hawes, M. S. Heard, S. J. Clark, A. M. Dewar, L. G. Firbank, J. N. Perry, P. Rothery, R. J. Scott, I. P. Woiwod, C. Birchall, M. P. Skellern, J. H. Walker, P. Baker, D. Bell, E. L. Browne, A.J.G. Dewar, C. M. Fairfax, B. H. Garner, L. A. Haylock, S. L. Horne, S. E. Hulmes, N. S. Mason, L. R. Norton, P. Nuttall, Z. Randle, M. J. Rossal, R.J.N.

Sands, E. J. Singer, and M. J. Walker. 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. 1. Soil-surface-active invertebrates. Phil. Trans. R. Soc. Lond. B. 358: 1847–1862.

Candolfi, M. P., K. Brown, C. Grimm, B. Reber, and H. Schmidli. 2004. A faunistic approach to assess potential side-effects of genetically modified Bt-corn on non-target arthropods under field conditions. Biocontrol Sci. Technol. 14: 1291–170.

Caprio, M. A. 2001. Source-sink dynamics between transgenic and non-transgenic habitats and their role in the evolution of resistance. J. Econ. Entomol. 94: 698–705.

Caprio, M. A., M. K. Fave, and G. Hankins. 2004. Evaluating the impacts of refuge width on source-sink dynamics between transgenic and non-transgenic cotton. J. Insect Sci. 4: 1–5.

Carrière, Y., C. Ellers-Kirk, M. Sisterson, L. Antilla, M. Whitlow, T. J. Dennehy, and B. E. Tabashnik. 2003. Long-term regional suppression of pink bollworm with *Bacillus thuringiensis* cotton. Proc. Natl. Acad. Sci. U.S.A. 100: 1519–1523.

Carrière, Y., M. S. Sisterson, and B. E. Tabashnik. 2004a. Resistance management for sustainable use of Bt crops in integrated pest management, pp. 65–95, *In* A. R. Horowitz and I. Ishaaya (eds.), Insect pest management: field and protected crops. Springer, Berlin, Germany.

Carrière, Y., P. Dutilleul, C. Ellers-Kirk, B. Pedersen, S. Haller, L. Antilla, T. J. Dennehy, and B. E. Tabashnik. 2004b. Sources, sinks, and the zone of influence of refuges for managing insect resistance to Bt crops. Ecol. Appl. 14: 1615–1623.

Cattaneo, M. G., C. Yafuso, C. Schmidt, C. Huang, M. Rahman, C. Olson, C. Ellers-Kirk, B. J. Orr, S. E. Marsh, L. Antilla, P. Dutilleul, and Y. Carrière. 2006. Farm-scale evaluation of transgenic cotton impacts on biodiversity, pesticide use, and yield. Proc. Natl. Acad. Sci. U.S.A. 103: 7571–7576.

Conner, A. J., T. R. Glare, and J. P. Nap. 2003. The release of genetically modified crops into the environment. Part II. Overview of ecological risk assessment. Plant J. 33: 19–46.

Dively, G. P. 2005. Impact of transgenic VIP3A X Cry1Ab Lepidopteran-resistant field corn on the nontarget arthropod community. Environ. Entomol. 34: 1267–1291.

Ferry, N., M. G. Edwards, J. Gatehouse, T. Capell, P. Christou, and A.M.R. Gatehouse. 2006. Transgenic plants for insect pest control: a forward looking scientific perspective. Transgenic Res. 15: 13–19.

Groot, A. T., and M. Dicke. 2002. Insect-resistant transgenic plants in a multi-trophic context. Plant J. 31: 387–406.

Jasinski, J. R., J. B. Eisley, C. E. Young, J. Kovach, and H. Willson. 2003. Select nontarget arthropod abundance in transgenic and nontransgenic field crops in Ohio. Environ. Entomol. 32: 407–413.

Lawrence, S. 2005. Agbio keeps growing. Nature Biotechnol. 23: 281.

Men, X., F. Ge, X. Liu, and E. N. Yardim. 2003. Diversity of arthropod communities in transgenic Bt cotton and nontransgenic cotton agroecosytems. Environ. Entomol. 32: 270–275.

Naranjo, S. E. 2005. Long-term assessment of the effects of transgenic Bt cotton on the abundance of nontarget arthropod natural enemies. Environ. Entomol. 34: 1193–1210.

Naranjo, S. E., G. Head, and G. P. Dively. 2005. Field studies assessing arthropod nontarget effects in Bt transgenic crops: introduction. Environ. Entomol. 34: 1178–1180.

Obrycki, J. J., J. E. Losey, O. R. Taylor, and L.C.H. Jesse. 2001. Transgenic insecticidal corn: beyond insecticidal toxicity to ecological complexity. BioSci. 51: 353–361.

Reed, G. L., Jensen, A. S., Riebe, J., Head, G., and J. J. Duan. 2001. Transgenic Bt potato and conventional insecticides for Colorado potato beetle management: comparative efficacy and non-target impacts. Entomol. Exp. Appl. 100: 89–100.

Riggin-Bucci, T. M., and F. Gould. 1997. Impact of intraplot mixtures of toxic and non-toxic plants on population dynamics of diamondback moth (Lepidoptera: Plutellidae) and its natural enemies. J. Econ. Entomol. 90: 241–251.

Schuler, T. H., G. M. Poppy, B. R. Kerry, and I. Denholm. 1999. Potential side effects of insect-resistant transgenic plants on arthropod natural enemies. Tibtech 17: 210–216.

Sisterson, M. S., and B. E. Tabashnik. 2005. Simulated effects of transgenic Bt crops on specialist parasitoids of target pests. Environ. Entomol. 34: 733–742.

Sisterson, M. S., R. W. Biggs, C. Olson, T. J. Dennehy, Y. Carrière, and B. E. Tabashnik. 2004a. Arthropod abundance and diversity in Bt and non-Bt cotton fields. Environ. Entomol. 33: 921–929.

Sisterson, M. S., L. Antilla, Y. Carrière, C. Ellers-Kirk, and B. E. Tabashnik. 2004b. Effects of insect population size on evolution of resistance to transgenic crops. J. Econ. Entomol. 97: 1413–1424.

Sisterson, M. S., Y. Carrière, T. J. Dennehy, and B. E. Tabashnik. 2005. Evolution of resistance to transgenic crops: interactions between insect movement and field distribution. J. Econ. Entomol. 98: 1751–1762.

Snow, A. A., D. A. Andow, P. Gepts, E. M. Hallerman, A. Power, J. M. Tiedje, and L. L. Wolfenbarger. 2005. Genetically engineered organisms and the environment: current status and recommendations. Ecol. Appl. 15: 377–404.

Whitehouse, M.E.A., L. J. Wilson, and G. P. Fitt. 2005. A comparison of arthropod communities in transgenic Bt and conventional cotton in Australia. Environ. Entomol. 34: 1224–1241.

Wold, S. J., Burkness, E. C., Hutchison, W. D., and R. C. Venette. 2001. In-field monitoring of beneficial insect populations in transgenic corn expressing a *Bacillus thuringiensis* toxin. J. Entomol. Sci. 36: 177–187.